OXFORD AVIAN BIOLOGY SERIES

THE SENSORY ECOLOGY OF BIRDS

GRAHAM R. MARTIN

Oxford Avian Biology Series

Oxford Avian Biology Series

Series Editor: Professor T.R. Birkhead FRS (University of Sheffield, UK)

A new series of exciting, innovative contributions from the top names in avian biology. Topics have been carefully selected for their wider relevance to both students and researchers in the fields of ecology and evolution.

Volume 1: Avian Invasions
Tim M. Blackburn, Julie L. Lockwood, Phillip Cassey

Volume 2: Interspecific Competition in Birds
André A. Dhondt

Volume 3: The Sensory Ecology of Birds
Graham R. Martin

The Sensory Ecology of **Birds**

Graham R. Martin
School of Biosciences, University of Birmingham

OXFORD
UNIVERSITY PRESS

OXFORD
UNIVERSITY PRESS

Great Clarendon Street, Oxford, OX2 6DP,
United Kingdom

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide. Oxford is a registered trade mark of
Oxford University Press in the UK and in certain other countries

First Edition published in 2017

Impression: 1

Published in the United States of America by Oxford University Press
198 Madison Avenue, New York, NY 10016, United States of America

British Library Cataloguing in Publication Data
Data available

Library of Congress Control Number: 2016951955

ISBN 978–0–19–969453–2 (hbk.)
ISBN 978–0–19–969454–9 (pbk.)

DOI 10.1093/acprof:oso/9780199694532.001.0001

Printed and bound by
CPI Group (UK) Ltd, Croydon, CR0 4YY

Dedicated to the memory of Marie-Anne Martin

Preface

It is just 100 years since the publication of the book which started the area of enquiry that has become known as Sensory Ecology. That book was *The Fundus Oculi of Birds*, written by the Canadian-born clinician, Casey Albert Wood. At the time of its publication Wood was Professor of Ophthalmology at the University of Illinois. Although he was a clinician, he had a passion for birds and he managed to combine his two interests in this book. A recent exhibition, 'The Bird Man of McGill', was promoted by the rare books and special collections section of McGill University. It presented information on Wood's life and his many interests. Wood gave his personal archive and collections to the University and now the exhibition can be readily browsed in digital form at http://digital.library.mcgill.ca/caseywood/.

Casey Wood employed a comparative approach to the study of birds' eyes. Using relatively simple techniques, he examined and described the eyes of a wide range of bird species held in various zoos. He viewed the eyes of live birds through a hand lens or an ophthalmoscope, and he also examined whole retinas of excised eyes using a microscope. Wood recorded in drawings, and in paintings executed by Arthur Head, some of the diversity in structures found in the retinas of birds. The book was of a large format and took as its inspiration some drawings published 20 years earlier by J.R Slonaker in a paper titled, 'A comparative study of the areas of acute vision in vertebrates' in the *Journal of Morphology.* Remarkably illustrations from both Slonaker and Wood still have value to anyone wishing to start describing the diversity of birds' eyes and also for anyone wishing to provide a framework that accounts for this diversity in both functional and ecological terms.

Wood's final conclusion in his book was, 'In future no report upon a particular avian species can be held complete that ignores the visual apparatus'. It is very clear that this conclusion still holds. Indeed all of the detailed understanding gained in the past century on the physiology, anatomy, function, and evolution of vision in birds has reinforced many times over the wisdom of Wood's conclusion. Yet many people still ask very general questions about 'What can birds see?' They often ask this because they have a general understanding that the sensory world of birds is in some way different from ours. They often ask in the hope that there will be just a few simple differences between our vision and the vision of birds, simple facts that can be readily learnt and perhaps be of value when faced with an applied question, such as how to prevent birds flying into obstacles, or getting trapped in fishing nets.

Today, we not only know about the diversity of vision among bird species, but we also have potent ideas that can be used to account for this diversity. We are also now gaining a clearer understanding of the capacities and diversity of the other senses of birds, of the trade-offs within a particular sensory capacity, and of the trade-offs and complementarity between different sensory information in the control of particular behaviours. For example, we now have ideas for understanding how hearing can complement vision in the execution of particular tasks, or touch sensitivity can complement vision in others.

One hundred years on from Wood's book is a good time to bring together much of what is known about the senses of birds. Much of this information can now be interpreted in the broad framework of what has become known as sensory ecology. From one perspective this whole book is an argument in support of Wood's final conclusion, but we can now broaden his conclusion and state that, 'No report upon a particular avian species can be held complete that ignores its sensory systems'. This captures the fact that birds are far more than animals guided by vision, while vision may often be the dominant sense, many senses come into play at any one instant. Furthermore, particular behaviours may, in fact, be controlled by information which at best can be described as sparse. In some important instances, birds conduct key behaviours when their senses provide what seems to be a paucity of information.

This book initially sets some broad questions and provides a brief historical perspective on how senses in non-humans have been understood. These are followed by some general surveys of the sensory capacities of birds. In the latter half of the book, this information is used to answer questions on the information that birds have available to guide the execution of key tasks. Finally, the question of why birds are often unable to meet novel challenges posed by humans is addressed. Throughout the book, many old assumptions about the sensory worlds of birds are challenged by the research findings which have been published since Woods' seminal work. There is much here to interest anyone who has more than a passing interest in birds, in sensory systems, or in behaviour. I also hope there is much that will challenge reader's assumptions about the sensory information that they use to control their own behaviours.

Acknowledgements

Individual acknowledgements of the people who have helped to complete this book are all but impossible. So many people have contributed in so many ways and over many years, to the ideas presented here. Colleagues, research collaborators, and students have all provoked my ideas, framed questions for me to ponder, and provided support and companionship throughout my career. They have all helped to give me the motivation and shored up my confidence when it came to putting this book together.

The most tangible help came from my late wife, Marie-Anne, who initially encouraged me to put it all down on paper in one place, and she encouraged me to carry on its completion even though she knew she would never see the result. She would have been my proofreader and indexer since those were her professional skills and I am sure the text will have ragged edges which she would never have allowed slip through.

Other specific acknowledgements are due to people who have allowed me to reuse and edit their illustrations and photographs to help clarify and enlighten the text. I hope I have acknowledged appropriately all of their specific contributions in the figure legends. A small number of people set me on the path which was to lead eventually to this book about avian sensory ecology. Ian Gordon, Bill Muntz, and John Lythgoe were all there encouraging me when I first started asking questions about birds' sensory capacities and the information that they provided. What they started off has continued to fascinate me for nearly 50 years. Sadly none of them is alive to see this book and provide the feedback and comments which they generously offered so many years ago.

Contents

1
Birds' Eye Views

1.1 Metaphor and Reality

The bird's eye view is popular. Referred to by media reporters, management gurus, and politicians alike, a bird's eye view has become a favoured short-hand way of referring to an overview, a new perspective on a scene, or a new way of considering a set of ideas. A bird's eye view implies many things: standing back, looking down from a height, or taking stock of a broad range of ideas. Clearly, as a way of placing things in a broader context, a bird's eye view can be both exciting and liberating. Birds' eye views are, however, not only used as a metaphor. While it must be true that every bird's eye has a real view of the world, people often speak as though we too can see and appreciate such real birds' eye views, and we seem to assume that birds have a special way of seeing the world from a high vantage point.

This assumption appeared to be made concrete by the pioneering systematic use of aerial photographs for military purposes in the Great War of 1914–18 (Barker 2002), which was further developed by archaeologists in the 1920s to reveal traces of human activity and objects hidden below the surface of the earth (Brophy and Cowley 2005). This evidence seemed to show convincingly that a bird's eye view could reveal hidden secrets and to show that in landscapes there are patterns which cannot be detected from the usual ground-based human perspective. Now the runaway success of satellite images, first in posters and books, and from the start of the 21st century everywhere on the internet, means that all of us, at the click of a mouse or the touch of screen can apparently get a real bird's eye view of anywhere on the planet. The worldwide success of Yann Arthus-Bertrand's *Earth from the Air* book and touring photographic exhibitions (Arthus-Bertrand 1999) showed at the end of the 20th century how exhilarating it was for people from many cultures to apparently see the world 'through birds' eyes'.

To free us from a grounded or ground-based existence in order to see more, or gather together ideas in order to understand connections, is clearly a richly rewarding experience. However, the search for such perspectives using the metaphor of a bird's eye view is not new; indeed it has a long history. What is new is that real aerial views are so readily available. Furthermore, because of advances in photography and imaging, they seem more complete, more real, more up-to-date, and so we feel

The Sensory Ecology of Birds. Graham R. Martin: Oxford University Press (2017).
 DOI 10.1093/acprof:oso/9780199694532.001.0001

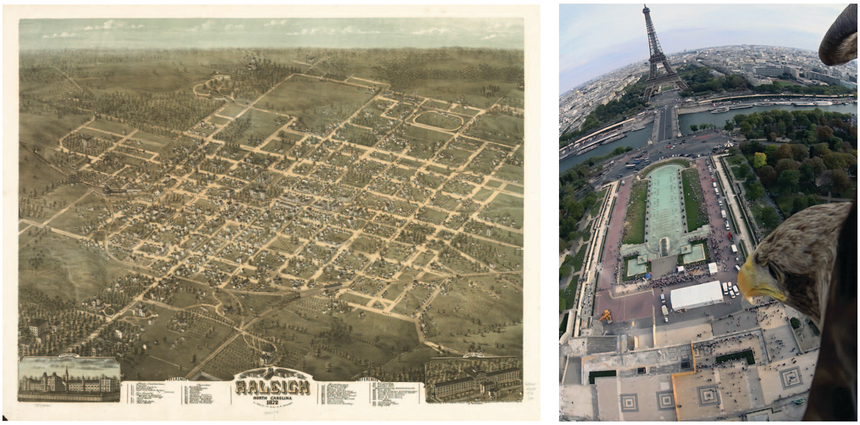

Figure 1.1 Bird's eye views. To the left an illustration published in 1872 under the title 'Bird's eye view of the city of Raleigh, North Carolina'. An imaginary perspective of how the town would look from the view point of a bird flying over, it is one of a series of similar 'bird's eye views' of towns in the eastern USA published at this time and was presumably inspired by views from a balloon. The collection is held in the Library of Congress, Washington, DC. Nearly 150 years later the same idea is still in use and exemplified by the image on the right, dated October 2014. It is from a press release publicizing a new camera under the title 'The 100% authentic Eagle Eye View'. The camera, mounted on the back of a White-tailed Eagle flying above Paris, looked over the bird's head towards the ground, (Credit SonySWNS.com Creative Commons).

more convinced that they do show us a real bird's eye view. They appear to show us how things actually appear to a bird as it flies over (Figure 1.1).

People have long thought of the view from a high promontory as equivalent to that of a bird, and once artists had mastered the art of perspective their imaginations led viewers to see scenes in new ways. Once flight was mastered by humans, seeing the scene from an ever-changing overhead viewpoint became thought of as even more bird-like, and the moving image captured on film in colour as an even more authentic bird's eye view.

Clearly it is an attractive liberation for humans to think in this way, to imagine that they are birds and can take it all in, to see their world in a broader perspective, and detect patterns that they had not seen before. But while we like to refer to this as a bird's eye view, does it really reflect what birds see? Do birds actually look down and take it all in? Do birds ever see the world as captured by the camera lens looking down from a crane arm, a balloon, an aircraft, or a satellite? Is it that simple?

What are real birds' eye views? How do birds see and experience the world, not only when they are flying over but when they are on the ground, foraging on a tree trunk, flying through woodland, or when they dive below a water surface? Each of these is also a bird's eye view. It is far from trivial to ask what do birds actually see as they fly over? Do they even look down and take it all in, or are they more interested in what is going on above, behind or out to the sides? Do birds attend constantly to what is below, and if so how much detail is evident to them? I will argue that there are in fact very many different birds' eye views. A bird's eye view depends not just upon what a bird is doing but it also depends very much upon the species through whose eyes we hope to view. It will also become evident that the way that we see the world is peculiar and particular to ourselves: the human eye view is as particular as that of the view of any species of bird. It will also become clear that our idea of a bird's eye view is not only quite different to those actually experienced by birds, but also different to those of all other animal groups. The general human-held idea of a bird's eye view is indeed just a metaphor; it would not be understood by any bird.

1.2 Many Birds, Many Views

The overall thesis of this book is not just that there are almost as many birds' eye views as there are species of birds, but also that the vision of each species is finely tuned to the tasks and the perceptual challenges which they face in their daily lives. My argument is that when account is taken of all the other sensory channels through which birds gain information about the world, it soon becomes apparent that each bird has available to them a complex array of information which underpins the performance of the plethora of tasks that constitute the life of birds. Birds do far more than fly and to do it all, they need diverse and complex sources of information.

At first glance this may seem rather bewildering. If there is so much variation between species, can anything be said that has general application? Can we extrapolate knowledge from one species and safely apply it to another? It will be argued here that there are indeed a number of powerful general principles and constraints which have worked to shape how birds gain information about their worlds. At base we must answer the question: 'What have been the drivers of natural selection that have led to the evolution of the many different birds' views of the world?' To understand these drivers we need to determine the functions that the senses of birds primarily serve. Is it flight, as has been commonly supposed, or reproduction, or foraging, or some other key activity in the lives of birds? What aspects of the natural environment really drive differences in vision and other senses between species, and how is vision used alongside, or in conjunction with, other senses in specific situations? In producing this broad perspective of constraints and drivers, we might be led to enquire just what human vision and our other senses are for: what has driven the selection of our own sensory capacities?

In trying to answer these questions, it is necessary to explore not just the diversity of vision and other senses but also the diversity of the environments in which senses have been shaped to operate and how they operate alongside each other. For example, natural light environments in any one place will vary over a very wide range of levels (potentially many millions-fold), the colour (or spectral distribution) of the ambient light regime can also vary dramatically, as also can the clarity of the scene due to particles and water vapour in the air. Furthermore, when a bird moves within a habitat or from one habitat to another (e.g. from air to water), the range and rate of transition between different sensory or perceptual challenges can be very dramatic and rapid. How do eyes, visual systems, and other sensory inputs cope, not only with specific challenges but also challenges that change?

It is also necessary to understand how information from the sense of vision has been compromised or limited by the very nature of light itself and the difficulties of capturing and extracting information from it: in short what are the ultimate limits of vision set by physics? Also how is sensory information from vision traded-off, compromised, or complemented by information gained from another sense? For example, how are vision and hearing, or vision and touch sensitivity in the bill, traded-off against each other to provide complementary information that helps a bird find food while staying safe from a predator?

One of the main problems in choosing to write about the diversity of birds' eye views, and for exploring the reasons for this diversity, is that birds are themselves a very diverse group of animals, a fact that is at the root of their fascination for us all. This general diversity does not, however, occur with respect to basic anatomy and physiology which are remarkably conservative (Baumel 1993; King and McLelland 1985). At a fundamental level, a chicken on a dinner plate is very much like the song bird in the garden, the grebe fishing in the local pond, or the shorebird probing in the mud of a foreshore. They may differ in size but all birds are built around the same basic anatomy, structure, and physiology. This is quite unlike the situation in other major vertebrate groups, such as mammals and fish, in which there are marked differences in all these features (Kardong 2014).

This conservatism among birds has been argued to be the result of fundamental constraints that arise from the requirements that limit all self-powered flying organisms and indeed all flying machines. These requirements are for the ability to achieve high power output combined with low body weight, both of which are necessary for getting off the ground, i.e. overcoming the power of gravity by exploiting the rather meagre properties of air to support weight (King and McLelland 1985). However, the embodiment of those basic conservative features common to all birds has allowed natural selection to shape birds into very diverse forms that are able to reach and exploit a remarkably wide range of habitats and resources across the Earth (Gill 2007).

This exploitation of many diverse resources has been achieved primarily through the evolution of diversity in body sizes and, importantly, through diversity in peripheral body structures: legs, wings, feet, and bills (Perrins 2009). Diversity among these is readily acknowledged and understood. They are explained as being the result of powerful selective pressures for the efficient exploitation of different resources, especially different foods. Indeed all ornithology textbooks contain chapters discussing and explaining the diversity of feet, wings, bills, etc., in terms of the physical and mechanical challenges that they have evolved to meet (Gill 2007; Perrins 2009; Podulka et al. 2004).

Explanations are now available, for example, of how the aerodynamic properties of different wing shapes result in very different flight capabilities and how these evolved to overcome challenges posed by the physics of flight and the mechanical properties of bones and feathers (Norberg 1990). But these different wing shapes are the result of variations within a very conservative forelimb structure, and it is clear that very subtle variations in size, shape, and mechanical properties of bones and feathers can result in quite different flying abilities. Similarly differences between species in their bill structures and shapes are the product of subtle variations in basic anatomy, which give rise to a rich variety of mechanical properties that are analogous to different human-invented materials and tools (King and King 1980; Podulka et al. 2004) (Figure 1.2).

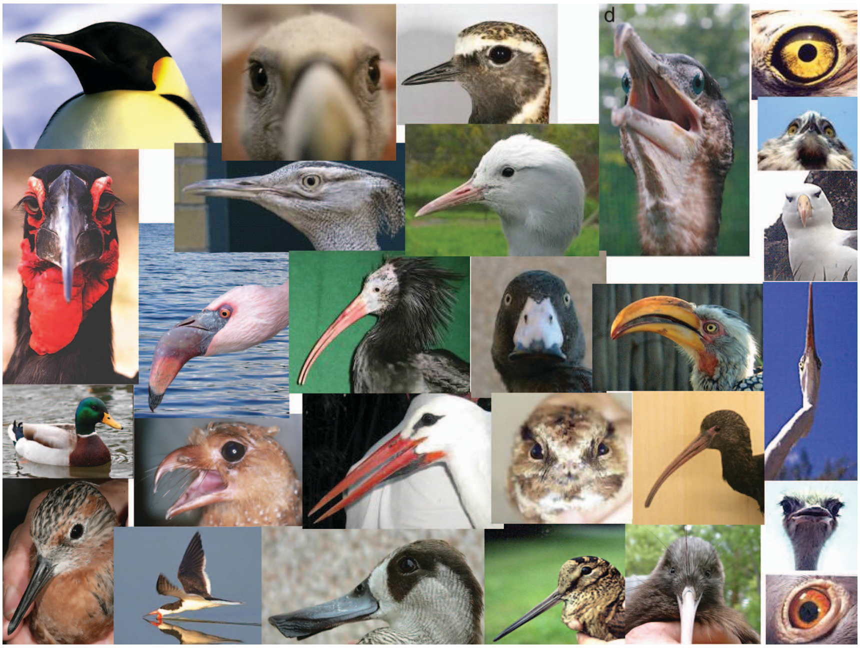

Figure 1.2 A plethora of birds' eye views? This montage shows a wide range of bird species whose vision and other senses have been investigated to various levels of detail. All of these species, and many more, feature in this book. At first sight, this montage captures the striking diversity of bill shapes and sizes and could easily be a prelude to a discussion of the mechanics, functions, and the evolution of bird bills. We would not be surprised by such accounts of the diversity of these bills. However, alongside these more obvious examples of diversity of bird structure is an equal diversity in the structures of the eyes and other sense organs in these same species. The diversity of these sensory structures tell their own story of function and evolution. Especially important is the provision of information for guiding these different bills in their execution of key tasks in the daily lives of these birds.

It is these differences in bill properties that facilitate the exploitation of very diverse food types by different species. There is now good evidence that subtle, but functionally significant, evolutionary changes to bill structure can occur very rapidly within a population in response to the relative availability of different food types. Indeed it has recently been demonstrated that evolution through natural selection can actually occur in 'real time' on these peripheral structures (Grant and Grant 2014; Weiner 1994).

All of these peripheral structures (wings, feet, and bills) can be regarded as functioning principally to ensure the efficient exploitation of environmental resources. This can be through efficient locomotion within and between different environments, and directly in the exploitation of food resources. To the diversity of these peripheral structures, I now add diversity of sensory systems, especially eyes, driven primarily by the informational requirements of efficient foraging.

1.3 The Tuning of Senses

The overall argument of this book is that the sensory systems of birds, and the information that they provide, exhibit differences which are just as subtle and functionally important as the mechanical differences between bills, wings, or feet. Of course, these subtle differences between sensory systems are less obvious and less readily catalogued. Their properties are more difficult to measure than the differences between the structures and mechanical properties of bills or feet. The functional differences between bird species in their sensory systems are less obvious, less readily understood. This book attempts to make these differences in the senses of birds more explicit, more readily understood.

It will be shown that there are many sources of independent variation within sensory systems and these sources of variation can be combined in different ways. Furthermore, this has allowed sensory capacities to become finely tuned to particular sensory challenges so that important variations can occur even between closely related species and, in turn, these can have important influences upon behaviour. For example, two duck species (Figure 1.3) of the same genus differ in a relatively minor way in their visual fields. However, these small differences have clear consequences for the foraging and vigilance behaviours of these birds (Guillemain et al. 2002). This shows that the interactions between tasks and the information used to control them can be significant, but the differences upon which they are based can be very subtle. Differences in the sensory capacities of these ducks, unlike the obvious differences in their bill structures, are not apparent from casual observation. However, differences in the information that these two species have available are as important for understanding their behaviours as the differences in their bill structures.

Figure 1.3 Subtle differences in sensory capacities. Two species of wildfowl which are closely related and placed in the same genus: Northern Shoveler *Anas clypeata* (left), Eurasian Wigeon *Anas penelope* (right). These birds differ in their feeding techniques and can be readily seen feeding in different ways, but often in the same locality. Shovelers and Wigeons differ quite obviously in the structure of their bills. The broader bills of Shovelers function to filter food items from the water's surface. This does not require bill position to be accurately positioned using vision. The narrower bills of Wigeons function primarily for selective grazing in short swards. This does require the bill to be placed accurately to grab small items. These differences in the requirements for bill placement are reflected clearly in differences in their vision and, in turn, this also influences marked differences in other behaviours, especially the time devoted to predator detection and vigilance behaviours (Chapter 8). Subtle tuning of information gathering for the efficient conduct of one task can clearly have important consequences for how information is gathered for other tasks and lead to differences in other aspects of behaviour. (Photo Credits, Pete Blanchard).

Like bills, feet, or wings, there is plenty of scope for variation in sensory systems. Eyes have three main structural and functional components that can be subject to independent evolution: the optical system which produces an image of the world, the retina which starts the analysis of that image, and the position of the eyes in the head. Although they all operate within broad limits, there is much possible variation within each of these components, so much so, that the diversity of eyes and their associated capacities is certainly as large as the possible number of species of birds which exist. Furthermore, as in other peripheral structures, there must be variation between individuals within a species. It is, of course, these within-species variations that provide the material upon which natural selection can act. This is similar to the within-species variations which can be more readily seen in the size, shape, and physical properties of birds' bills, or the sizes and shapes of bones of the foot—features which are routinely measured as an index of variation within a species.

At core, birds may be rather conservative but we readily recognize that diversity in peripheral structures has led to the wonderful diversity that holds our attention and intrigues us all. Diversity in sensory systems, especially eyes, is no less intriguing and important for a full understanding of what birds are. There is, however, also variation in the other main sensory systems, including hearing, olfaction, taste, and touch.

The ears of birds, like those of all vertebrates, are hidden deep within the skull (Podulka et al. 2004). Casual observation might suggest that most birds do not even have ears, in that there are no obvious structures on the head associated with hearing. Even for the tutored eye, birds' ears are indicated only by a small group of feathers that hide the ear openings which are positioned just behind and below the level of the eyes. But ears within the skull may show diversity with respect to the length of the cochlea and the size and configuration of the bones of the middle ear. These can result in subtle differences in hearing capacities. Although most birds lack outer ears, those that do have them show remarkable abilities for the location of sounds (Norberg 1978; Payne 1971). Birds that lack these structures are relatively poor at sound localization. If attention is also paid to other sensory structures associated with the head, such as the clusters of touch-sensitive receptors found round the tip of the bill in some species (Berkhoudt 1980; Cunningham et al. 2010; Cunningham 2010; Piersma et al. 1998), then further diversity in the range of information that can be detected can be added to the information provided by the eyes.

When differences between these three main sensory systems: eyes, ears, tactile receptors, are taken into account, it seems very possible that not only are there different birds' eyes views, but each species actually lives within a unique sensory world, able to detect and respond to different information about the world that surrounds them. Understanding these worlds, why and how they differ, and how they may influence behaviour, is the challenge at the heart of this book.

I intend to take the reader through a series of arguments which I hope will leave them agreeing that we can talk only of birds' eye views, not the bird's eye view. Also I will demonstrate that the idea of a bird's eye view with which the chapter opened is indeed only metaphorical. I will also argue that when it comes to understanding the main factors which have shaped the evolution of vision in birds, the control of flight is perhaps something of an afterthought, something which is achieved within sensory parameters determined primarily by other factors. Flight, which is often portrayed as the very essence of birds, may not be controlled by special adaptations of the sensory systems. In fact, flight is probably controlled within constraints imposed primarily by the requirements for controlling not the position of the whole body, but by the exacting requirements for controlling the position of just a small part of it, the bill. Furthermore, these requirements for controlling bill position are balanced against a usually antagonistic requirement for the detection of predators. The control of general body position, as in flight, must be achieved within these more exacting requirements.

Working through this set of ideas requires a broad comparative context, and there is always need for data from a wider range of species in order to fully explore those general principles which provide the base upon which variation occurs. Once adopted, this comparative approach inevitably casts our own sensory systems, and the information that we use to control our own behaviour, in a new light. The conclusion is that humans too possess a special set of variations in the basic sensory systems of vertebrates, with the inevitable conclusion that the world which we inhabit is just as peculiar or special as that of other species.

In short, all animals share the same planet but they live in different worlds. The human perspective of the world is as specialized or peculiar as is that of other species. One of humankind's most striking primate features, two large eye set in the front of the head, is rather unusual. Furthermore, our retinas have a specialized set of photoreceptor cells arranged in a particular pattern. The result of our unusual eye positions, coupled with the features of our retinas, is that what we consider to be the 'normal' view of the world, a view in which the region of best resolution and best colour vision lies directly ahead, is far from typical. Human senses do not provide a monopoly on the reality of the world, nor do they provide a baseline from which all other species' views can be considered to deviate.

1.4 Epicurus, Sextus, and the Sceptics

That human senses do not provide a fixed reality of the world is not a new notion. The Greek philosopher Epicurus (341–270 BCE) (Figure 1.4) recognized that the senses, especially vision, place very real constraints not only on our overall understanding of the world but also shape how our personal worlds change from moment to moment (Warren 2009). This notion that our senses bring us ever changing information about even the same objects was crucial to Epicurus' system of ideas. It is a notion that has been discussed many times since; it was elegantly rehearsed with reference to the 'reality' of a wooden table by Bertrand Russell in his discussion on 'the uncertain nature of observed reality' (Russell 2001). However, it is a notion that is easily overlooked in the very anthropocentric world of today, a world that for most people is experienced without reference to other animals. It is also a world that for many people is captured by others through a camera lens and viewed on a screen, rather than from direct personal experience. Although Epicurus argued that human reality is always changing and uncertain, he did so from a purely human perspective. The Roman philosopher Sextus Empiricus (Figure 1.4) extended the insights of Epicurus to the world of non-human animals. In so doing, his arguments led to a way of understanding the world and to a philosophical framework whose application underpins the pervasive scientific world view of the present time.

Sextus Empiricus lived between c. 160 and 210 CE (Bailey 2002). He wrote many works, and many of his arguments were built upon ten principal observations (referred to as modes). These modes elaborated upon the ideas of Epicurus and on those of another earlier Greek philosopher Aenesidemus (who lived in

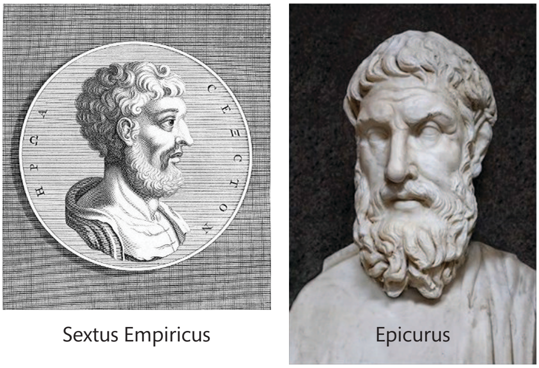

Figure 1.4 The ancient founders of sensory ecology. The Greek philosopher Epicurus recognized that humans and other animals differed in the information that they had available to them about the world in which they lived. He argued that this placed a severe limit on defining 'reality'. Sextus Empiricus expanded these ideas and used them to form the basis of his philosophical ideas of Scepticism.

the 1st century BCE). The writings of Sextus have become recognised as the best argued foundation for Scepticism, a still potent system of philosophy, indeed a whole approach to understanding life and the human condition (Popkin 2003).

Scepticism can be summarized as: 'neither affirm any belief as true nor deny any belief as false', an uncomfortable position for some people, but one which now lies at the heart of using science to understand the world.

The ten modes upon which Scepticism is based all address problems produced by the senses. The first three state:

- The same impressions are not produced by the same object owing to the differences in animals.
- The same impressions are not produced by the same object owing to the differences among human beings.
- The same impressions are not produced by the same objects owing to the differences among the senses.

Clearly the sceptical position is based upon a comparative approach, a cross-species approach, to the senses. It is also based upon recognition that the sensory systems of all animals differ one from another. From this, it is concluded that humans cannot ever be sure about the world. This is because what is known about the world is very different depending upon what information different senses provide, even about the same set of objects. In short, different senses provide different information, and different animals have different senses, so where does reality lie? The sceptics worked from these observations to arrive at a position which argues that it is not possible for humans to either affirm or deny any belief; in modern terms we must 'keep an open mind', because at a very fundamental level we cannot trust our senses to provide a foundation for certain truth about the world.

The sceptical system is underpinned by comparisons with emphasis upon differences among animals, among humans, and among the senses. But while the early sceptics could assert that there were such differences, they based this upon their own observations and upon the application of reason, they could not quantify these differences nor could they say how or why these differences came about. Today we have a range of techniques to enquire about the differences between the same senses in different animals. It is now possible to piece together diverse information to actually quantify differences in sensory information between different animals.

In addition, an evolutionary framework, driven primarily by the idea of natural selection, now gives us a way of understanding why and how these differences have come about. We have also acquired tools to enquire about the types of behaviour that different sensory information controls directly or indirectly. In essence, much of this book is about what has been learnt since Sextus was writing. The sceptical conclusions of Sextus have been reinforced, not diminished, by our modern understanding of sensory capacities and the reasons why they differ between animal species.

1.5 Sensory Ecology

The enterprise of fleshing out these differences, and understanding the reasons for them, falls within the broad subject of sensory ecology, which can be summarized as, 'The investigation of the information that underlies an animal's interactions with its environment' (Dusenbery 1992). David Dusenbery elaborated this approach in his book *Sensory Ecology: How Organisms Acquire and Respond to Information*.

The premises upon which sensory ecology is based clearly have their roots at least two thousand years ago in the writing of Epicurus and Sextus Empiricus. However, really important developments had to wait until the middle of the 19th century when Alfred Russel Wallace and Charles Darwin formulated the idea of evolution through natural selection. This put the enterprise of understanding why and how differences had arisen between animals, including differences in their senses, within a more certain framework.

Early works that looked into describing the differences between the senses of species, and how they were related to the perceptual challenges posed by different environments, first took shape with the publication of Casey Albert Wood's *The Fundus Oculi of Birds* in 1917 (Wood 1917). Wood (Figure 1.7) took a comparative, and what can now be described as a sensory ecology, approach. He was a Canadian-born clinician and Professor of Ophthalmology at the University of Illinois, but

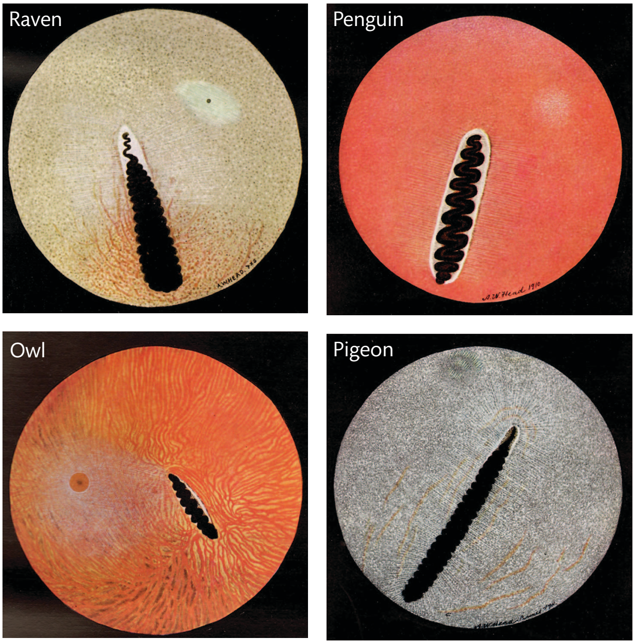

Figure 1.5 Diversity of birds' eyes. Four examples of the retinas of birds as viewed through an ophthalmoscope and portrayed in paintings in the book *The Fundus Oculi of Birds*, which was published 100 years ago (Wood 1917). The large black structure in each illustration is the pecten which extends out of the surface of the retina into the chamber of the eye (see Chapter 2 and Figure 2.1 for an explanation of the function of a pecten). The colours are genuine and modern photographs using a fundus camera show the same patterns. Clearly there is much diversity in all aspects of what is observed in these eyes. However, providing functional interpretations of this diversity is not straightforward. Wood concluded that every eye is different and warrants further investigation of its structure, physiology, and capacities, and in turn how these relate to behaviours and habitat characteristics. Shown here are 4 of the 53 species illustrated by Wood; each one has a different appearance. Raven: Northern Raven, *Corvus corax*; Penguin: African Penguin, *Spheniscus demersus*; Owl: Tawny Owl, *Strix aluco*; Pigeon: Common Wood Pigeon, *Columba palumbus*.

with a passion for birds. He used relatively simple techniques to examine and describe the eyes of a wide range of bird species. He viewed their eyes through a hand lens or ophthalmoscope, and also examined whole retinas of excised eyes using a microscope (Figures 1.5 and 1.6). Wood recorded in drawings and paintings some of the diversity in structures that he found in the retinas, including multiple foveas and elongated areas of high visual resolution. He described the eyes of more than 50 species to provide comparisons across phylogeny and broad characteristics of different environments. Crucially, he proposed ideas as to the functions of the different types of retinal organization that he identified. He suggested

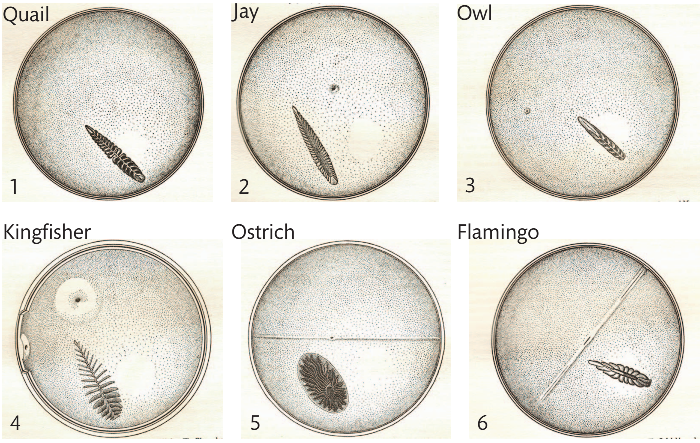

Figure 1.6 Diversity of birds' eyes. Six further examples of the retinas of birds viewed through an ophthalmoscope from Wood (1917). These series of illustrations emphasize structures which provide heightening spatial resolution within the field of view of the eye. Wood examined the eyes of 32 species in this way and reduced the diversity down to six main types in a sequence from least to most complex. Wood's examples of each type are presented here. In Type 1, there does not appear to be any region specialized for higher resolution vision; illustrated by California Quail *Callipepla californica*. Type 2 contains a single fovea in which the density of photoreceptors cells are increased and the retina is thickened (see Figure 2.8); the fovea is more or less centrally placed and so the region of highest visual resolution looks out along the axis of the eye; illustrated by Steller's Jay *Cyanocitta stelleri*. Type 3 is similar to type 2, but the region of higher acuity is displaced away from the centre of the retina and looks slightly more forwards in the field of view; illustrated by Western Barn Owl *Tyto alba*. Type 4 contains two regions of high resolution, one central and the other in the far periphery of the eye's field of view; illustrated by Common Kingfisher *Alcedo atthis*. Type 5 contains a linear area of enhanced resolution which runs in a band across the entire retina with a well-defined fovea placed more or less in the centre; the band is oriented approximately horizontal in some species (as illustrated here) but it can also be oblique; illustrated by Common Ostrich *Struthio camelus*. Type 6 contains a linear area and more than one fovea-like structures situated within the linear area; illustrated by Greater Flamingo *Phoenicopterus roseus*.

retinal organization could be divided into six main types (Figure 1.6). Among his conclusions was: 'The fundus oculi of Birds exhibits a great variety of areas of distinct vision, and these correspond closely to the habits and habitat of these animals—especially their methods of obtaining food, of escape from enemies, of migration, of reproduction, etc.' (p. 7). He also cautioned that 'Domestication or prolonged captivity brings about abnormal changes in the eye-ground of Birds, so that only healthy, wild specimens should be utilized in this or a similar research.' His final conclusion was that 'In future no report upon a particular avian species can be held complete that ignores the visual apparatus.' Thus, Wood was one of the first people to adopt a sensory ecology approach to understanding the function and diversity of birds' eyes, and to recognize that understanding senses is fundamental to understanding the biology of each species. A century after their publication, Wood's conclusions still hold. Furthermore, his illustrations still provide an intriguing catalogue of diversity in the gross structure of birds' eyes, and they continue to be a source of questions concerning how different species extract information from the world.

The next landmark publication was Gordon Lynn Wall's (1942) book *The Vertebrate Eye and its Adaptive Radiation* (Walls 1942) (Figure 1.7). This book was

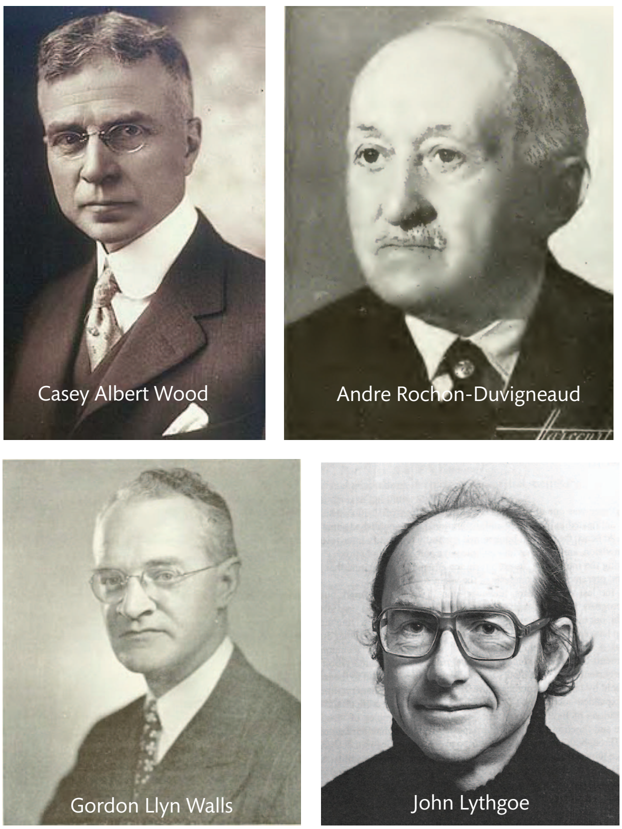

Figure 1.7 Twentieth century founders of sensory ecology. All four of these scientists played a key role in identifying, describing, and analysing the perceptual challenges posed by life in different environments. They also described and analysed how these challenges had been met by the evolution of differences in sensory systems and sensory capacities across the animal kingdom.

published in the year that Casey Wood died. Although concentrating only upon vertebrate eyes, Wall's book set a standard of breadth and depth in a single volume on senses that has, perhaps, not been surpassed. His volume contained 785 pages with an index taking up 60 of them. Many of the index entries are about individual species and reveal the broad taxonomic base of the comparative approach that Walls adopted. Given the growth in knowledge about how eyes work and what they can do, a modern publication covering the same ground as Walls' book would now have to be multi-volume. Indeed, although taking a more focused approach to particular senses and concentrating much upon humans, a six-volume series, extending to some 4200 pages, *The Senses* was published in 2008 (Basbaum et al. 2008).

Such has been the importance of Wall's book that it is still cited today, not only because it provides clear enunciation of some key hypotheses linking form and function of eyes, but also because it contains the only information available on the eyes of many species. Walls ranged widely and brought together all that was then known about vertebrate eyes, their structure, physiology, and evolution, and very much of what he described still stands. However, Walls was not particularly concerned about what eyes actually did for the animals that possessed them; he was more concerned with relationships between anatomy, physiology, and function. While Walls' main concern was with the features which made eyes specialized for different abilities (e.g. for the detection of colour or spatial detail), he was less concerned with how those abilities facilitated or constrained the behaviour of the particular animals that possessed them.

André Rochon-Duvigneaud published *Les Yeux et la Vision de Vertébrés* in 1943 (Rochon-Duvigneaud 1943), one year after Walls' book (Figure 1.7). At the time of publication Rochon-Duvigneaud was 80 years old. He had retired from clinical practice as an ophthalmologist 17 years earlier and had devoted his retirement to comparative studies of the structure of the eyes of a wide range of vertebrate animals. This book was the result; he published few papers on these topics. Like Walls' study, the book was framed around a broad comparative approach and took what would now be seen as a sensory ecology framework to investigate questions of diversity and function. Also, like Walls', the book was encyclopaedic in approach and ran to over 700 pages. However, Rochon-Duvigneaud's book was never published in English and it did not become as widely known as Walls'. These books complemented each other and a joint publication covering all of the material would have been a marvellous compilation. The two authors were of different generations. Walls graduated with his first degree in mechanical engineering at Tufts University (Boston, Massachusetts), in 1926, the same year that Rochon-Duvigneaud retired from his practice in clinical medicine at the Hotel-Dieu in Paris. It is intriguing that they must have been working on their books in parallel—one at the start of his career as a young man at Wayne State University, Detroit, the other during his second career in retirement in Paris.